Association between competition and facilitation processes and vegetation spatial patterns in alpha steppes

ALADOS, C. L. [1], GOTOR, P.[1] BALLESTER, P. [1], NAVAS, D. [2], ESCOS, J. M.[3], NAVARRO, T [2]. & CABEZUDO, B. [2]

[1] Instituto Pirenaico de Ecología. Avda. Montañana 1005. Apd. 202. 50080 Zaragoza, Spain. alados@ipe.csic.es

[2] Dpt. Biología Vegetal. Universidad de Málaga. Apd. 59. 29080 Málaga. Spain.

[3] Infraestructura & Ecología. Avda. Cardenal Herrera Oria, 65 3ª pl. 28034. Madrid, Spain.

Abstract. In semi-arid ecosystems, the self-organized spatial patterns of plants associated with catastrophic shifts can emerge from a variety of processes. In this study, on moderate slopes where *Stipa tenacissima* cover was high, the self-organization of some of the typical species of semi-arid Mediterranean matorral (*Phlomis purpurea*, *Sideritis oxteosylla, Heliantemum almeriense*, and *Brachypodium retusum*) was negatively correlated with *Stipa* cover. The extent of *Stipa* cover did not affect desert pioneer species, such as *Artemisia herba-alba*, *Fagonia cretica*, and *Launaea lanifera*. On pronounced slopes, the self-organizing structure of brushwood vegetation did not vary predictably with the amount of *Stipa* cover. We examined the competition/facilitation processes associated with self-organizing patterns in the dwarf-shrub (*P. purpurea*) and the half-shrub (*H. almeriense*). The developmental stability of *H. almeriense* was positively correlated with *Stipa* cover, which was expected because they are associated species in this seral thyme brushwood community. Indeed,

facilitation processes were manifested by the developmental stability increases under

Stipa canopy, particularly on high slope areas, where *Stipa* is less competitive. In *P.*

purpurea, negative feedback processes from competition with *Stipa* were manifested

where *Stipa* cover was high and on low slopes (developmental instability increased). In

general, competition with *Stipa* on low slopes tended to decrease plant self-

organization.

Nomenclature: The scientific names of species are according to Flora Europaea

(Tutin et al. 1972), Med. Checklist (Greuter et al.1984-89), and Flora Iberica

Castroviejo et al. (1986/2003).

Key words: Developmental instability, Fractal, Spatial patterns, *Stipa tenacissima*

Running head: Self-organizing spatial patterns in alpha-steppes

INTRODUCTION

The spatial patterns of plant distribution are the result of processes that operate on

multiple scales, and include topography, soil quality, availability of water and nutrients

(Couteron & Lejeune 2001; Rietkerk et al. 2002a), plant dispersal (Greig-Smith 1983;

Pacala & Silander 1985), and interactions among individuals (Wu et al. 1985, Cale,

Henebry & Yeakley 1989; Alonso, Bartumeus & Catalan 2002). The patches of

vegetation that result can be homogeneous, periodic (striped, spotted, or arc-shaped

patterns), scattered, or bare-ground. Those emergent patterns are manifested at spatial

scales that are larger than the spatial scales of the processes that generate them (Kolasa

& Pickett 1991; Martens, Breshears & Meyer 2000; Peterson 2000) and can be used to

detect important shifts in ecosystem processes before there is an irreversible switch in

ecosystem dynamics. Spatial self-organizing processes are described by Peterson (2002), who used a simulation model in which increasing ecological memory (the degree to which an ecological process is shaped by previous modifications of a landscape) increases the strength and spatial extent of landscape patterns.

A variety of processes is attributed to be the mechanisms of pattern formation in semi-arid ecosystems. Soil infiltration and nutrient retention around the plant crown promote facilitation in semi-arid vegetation (Bertness & Callaway 1994; Pugnaire, Haase & Puigdefábregas 1996; Pugnaire, Armas & Valladares 2004; HilleRisLambers et al. 2001). In contrast, soil erosion and run-off increase when vegetation cover decreases (Elwell & Stocking 1976). Consequently, there is a positive feedback between reduced plant growth and reduced water and nutrient availability (Rietkerk & Van de Koppel 1997), which can contribute to irreversible destruction of vegetation and emergent self-organized spatial patterns associated with catastrophic shifts (von Hardenberg et al. 2001, Rietkerk et al. 2002b, Rietkerk et al. 2004). Additionally, those patterns can emerge from the balance between competition and facilitation under strictly homogeneous and isotropic environmental conditions (Lefever & Lejeune 1997; Lejene et al. 2002).

Spatial patterns have an important effect on ecosystem function. Mathematical models demonstrate that, in water- or nutrient-limited ecosystems, pattern formations lead to higher average plant persistence than do homogeneous landscapes (von Hardenberg et al. 2001, Rietkerk et al. 2002b, Rietkerk et al. 2004). Spatial patterns can facilitate the coexistence of species by concentrating low-density species in areas where their rates of increase are higher. Spatial patterns in nutrient supply can increase the yield of individual plants (Pickett & Cadenasso 1985; Hutchings & Wijesinghe 1997; Wijesinghe & Hutchings 1999; Adler, Raff & Lauenroth 2001) and populations (Day,

Hutchings & John 2003a), relative to homogeneous conditions where the nutrient supply is similar. Apparently, that occurs because interplant competition is higher in homogeneous than in non-homogeneous environments because all of the parts of habitats are heavily exploited. In heterogeneous treatments, however, plants in nutrient-poor patches remain small, but they are more likely to survive than are those in homogeneous treatments (Day, Hutchings & John 2003b). In addition, the combined effects of spatial self-organizing and the greater likelihood of relatedness among neighbours favour community-level selection (Johnson & Boerlijst 2002).

To develop conservation strategies, it is important to understand the self-organizing capacity of the system. Here, we evaluate changes in vegetation spatial patterns in response to increases in *Stipa tenacissima* L. cover and the competition/facilitation processes associated with those changes. Gradual slopes favour tall grass steppe, whereas steep terrain favours brushwood (Alados et al. 2004a), and dominant competition reduces the degree of self-organization (Cale et a. 1989). We hypothesize that characteristic species of the brushwood vegetation will reduce self-organized patterns in response to increases in *Stipa* cover on low slopes, where *Stipa* is highly competitive, and that the associated competition and facilitation mechanisms can be responsible for self-organizing patterns.

To test that hypothesis, first we analyzed the relationship between *Stipa* cover and the diversity and heterogeneity of the ecosystem. *Stipa* is the most successful species in semi-arid southeastern Spain because of its reproductive strategy, which is based on sexual and asexual reproduction (Hessen 1999), and its capacity to retain soil and minimize runoff, especially in fine-material soils (Cammeraat et al. 2002). We predict a negative correlation between *Stipa* cover and plant diversity, and a positive correlation with the homogeneity of plant spatial distribution. The more homogeneous the spatial

distribution, the fewer gaps available for new colonizing species (Hutchings et al. 2003).

Where the slope gradient is high, perennial bunch-grasses also disappear because of the loss of fine material, which leaves the root exposed and reduces the survival of species that have shallow roots, such as perennial grasses. In contrast, woody species that have deeper roots can survive on pronounced slopes that have greater stoniness and rugosity (Hodgson et al. 1994; Guerrero-Campo et al. 1999). As such, slope gradient is an important factor influencing vegetation succession in semi-arid areas. We predict that pronounced slopes maintain the self-organizing structure of brushwood vegetation, independently of the amount of *Stipa* cover. Conversely, on moderate slopes, where *Stipa* is better adapted, negative feedback processes that arise from competition might decrease the self-organization of brushwood species in response to higher *Stipa* cover. To test that prediction, we used Detrended Fluctuation Analysis (Peng et al. 1992) to compare the degree of spatial aggregation of each species on pronounced and moderated slopes along a gradient of *Stipa* cover.

Spatial self-organization can be related with scale-dependent facilitation and competition associated to the redistribution of a limiting resource (Rietkerk et al. 2004). Positive feedback from facilitation processes can lead to self-organized vegetation patterns in arid ecosystems (Rietkerk et al. 2002b) as opposed to the random patterns arising from competitive interactions (Cale et al. 1989). Positive feedback from facilitation processes with *Stipa* can lead to self-organized vegetation patterns when its competitive ability is reduced in less favourable habitats. We predict that plants living around *Stipa* are in better condition than are those in gaps on higher slopes, but the opposite occurs on moderate slopes, and those trends are more evident as *Stipa* cover increases. To test that prediction, we analyze the differences in the stress response of

plants living under *Stipa* canopy vs. gap along *Stipa* cover gradient in two contrasting slopes. We used Developmental Instability as an indicator of stress in individual plants.

METHODS

Study Area

This study occurred in the Cabo de Gata Natural Park (37 570 ha), southeastern Spain, which was founded in 1987. Elevation ranges from sea level to 493 m at El Fraile peak, and the climate is Mediterranean semi-arid. Between 1973 and 1996, the average annual rainfall at 43 m asl was 193.9 mm, and the mean annual temperature was 19.4ºC. In the area, the potential vegetation is a dense matorral of *Pistacia lentiscus* L., *Chamaerops humilis* L., and *Rhamnus lycioides* L. Historically, the area was exploited mainly by traditional agro-pastoral systems, with cereal cultivation on the floodplains and livestock (sheep and goats) grazing on the slopes.

We selected four sites that had different degrees of *Stipa* cover, and ranked them in order of increasing *Stipa* cover, from 1 to 4 where the slope was low, which is the preferred habitat of *Stipa* (Fig. 1). Two slopes were selected at each site; one was <10º (low) and the other was between 20º and 30º (high). According to Berael et al. (1995), 9º is the critical slope for incipient rill formation. We selected sites that had similar soil types and exposures based on previous landscape analyses (Alados et al. 2004a), and we assume that changes in plant spatial patterns reflect spatial self-organizing processes that arise from local interactions between neighbouring individuals and local dispersion.

Data collection and analysis

Spatial pattern analysis

From 15 to 30 April 2003, we surveyed the vegetation at the sites. We randomly selected 32 transects that were 500 m long (4 per site and slope) and parallel to the slope line. To estimate plant abundance and richness in each transect, we used the line intercept method (every 20 cm). To prevent noise caused by an increase in annual species in the highly disturbed site, we grouped annual species (Alados et al. 2003).

The *Proportional diversity* H' index integrates richness and evenness using the Shannon Information Index (Shannon 1948). The probability that a given species occupies a transect (p_i) is scale-dependent; i.e., $H'_{(\varepsilon)}$ changes with window size (ε),

$H'_{(\varepsilon)} = \sum_{i=1}^{N_{(\varepsilon)}} p_i \ln \frac{1}{p_i}$. We calculated the *Information Fractal Dimension*, D_I, at a series of

scales of size $\varepsilon = 2^n$, for n from 0 to 6, i.e., 1, 2, 4 … 64 m, where $D_I \cong \lim_{\varepsilon \to 0} \frac{H'_{(\varepsilon)}}{\ln 1/\varepsilon}$

(Farmer, Ott & Yorke 1983). The values are constrained between 0 and 1 because we obtained the fractal dimension from linear transects (1-dimension).

To measure the distribution pattern of each species, we used *Detrended Fluctuation Analysis* (DFA). We determined the degree of spatial aggregation of each species' cover, independently of the scale of measurement. The root-mean-squared fluctuation of integrated and detrended spatial presence distribution from contact points along a 2050-point transect was measured at different observation windows and plotted against the size of the observation window on a log-log scale. The details of the methods are described elsewhere (Peng et al. 1992; Alados & Weber 1999). Basically, the integrated sequence $y(s) = \Sigma_i z(i)$ is subdivided into non-overlapping sequential sets or "boxes" of b point contacts ($z(i) = +1$ for presence, $z(i) = -1$, for absence). A regression line is fit for each box of size b; i.e., we regressed $y_b(s)$ on s, and calculated the residual variance

per each box size, $F^2(b) = \dfrac{\sum (y_b(s) - \hat{y}_b(s))^2}{N}$. To provide the scale of the relationship

$F(b) \propto b^\alpha$, that process was repeated for scales 4, 6, 8 …. 512 along the first 2050 points of each transect.

The α parameter represents the long-range correlation of the plant distribution sequence, which is equivalent to the Hurst exponent (Hausdorff et al. 1997). Theoretically, α is not affected by the magnitude of fluctuations, but only by the sequential ordering of the fluctuations. If $\alpha > 1/2$, the sequence depends on the history of the distribution itself, and when $\alpha = 1/2$, the sequence is randomly distributed.

Competition/facilitation processes generating vegetation spatial patterns

To analyze changes in competition/facilitation mechanisms in response to environmental conditions, we used a 2 x 2 x 3 factorial design to compare the effect of slope (< 10º and between 20º-30º) and competition/facilitation interactions (gap *vs.* underneath *Stipa*) on the morphological responses of three populations of *Helianthemum almeriense* Pau that had different levels of *Stipa* cover (High in Site 4, Medium in Site 2 and Low in Site 1). Similarly, we performed a 2 x 2 x 2 factorial design for two populations of *Phlomis purpurea* L. (High in Site 3 and Low in Site 2). We selected 30 plants of each species per case factor in two parallel transects (15 plants per transect), which totalled 240 *P. purpurea* and 360 *H. almeriense*. To reduce variability in the analysis we chose similarly sized adult plants. We collected three seasonal shoots from different branches of each *P. purpurea* and *H. almeriense*.

Translational symmetry measures the relationship between internode length and node order, which follows a self–similar sequence in which internode order declines regularly up the stem (Alados et al. 1998; Escós, Alados & Emlen 1997). Beginning from the shoot

base, the relationship between internode length (*L*) and node order (*N*) fits the general equation, $L = kN^a e^{-bN}$, where *e* is the natural base, and *k, a,* and *b* are fitted constants. The constants of the equation were obtained from regression analyses. Under stress, the impact of random perturbations increases, which leads to greater developmental instability and a decrease in the accuracy of the curve fitting. Developmental instability was estimated using the adjusted coefficient of determination R^2, the standard error of the regression (Syx), and the standard error of the parameter *a* (Sa).

H. almeriense has short seasonal shoots and single terminal flowers. *P. purpurea* has long seasonal shoots and terminal verticillate inflorescences. From both species, we selected seasonal shoots, measured shoot length, and internode length from the base to the top using an electronic calliper to the nearest 0.01 mm.

Before the analysis of variance, translational asymmetry parameters were averaged per individual. Treatments were compared using a mixed-model ANOVA having three fixed effects and one level nested analysis (transect nested within treatment). When we detected interactions among treatments, we performed a partitioned analysis of variance. To compare treatment means, we used Tukey's studentized range test. Means ± se are presented in figures.

RESULTS

Plant spatial patterns

Proportional diversity (H') integrates species richness and evenness in a single index. We regressed Shannon Index values against the amount of *Stipa* cover for all treatments using a reduced major axis regression because both variables were measured with error. Proportional diversity significantly negatively correlated with *Stipa* cover (Fig. 2). The

95% confidence intervals for the slope were -1.67 >-3.50 >-58.19. The adjusted coefficient of determination from the orthogonal contrast was $R^2 = 0.22$.

The Information Fractal Dimension (IFD) quantifies the degree of heterogeneity, independently of the scale. The major axis regression between *Stipa* cover and IFD confirmed a positive correlation between the homogeneity of plant distribution and *Stipa* cover (Fig. 2). The 95% confidence intervals for the slope were: 3.41 > 0.233 > -1.09. The adjusted coefficient of determination using the orthogonal contrast was $R^2 = 0.60$. We expected more species to invade the community as more gaps became available and the major axis regression confirmed this expectation. The Shannon Index was significantly negatively correlated with plant homogeneity distribution (IFD). The 95% confidence intervals for the slope were: -7.07 > -9.48 > -14.34. The adjusted coefficient of determination obtained from the orthogonal contrast was $R^2 = 0.55$.

The DFA describes patch-species connectivity by providing information about fragmentation, spatial autocorrelation, and patchiness. The organization of seral-thyme heliophyllous species (such as *P. purpurea*, *Rosmarinus officinalis*, L., *Thymus hyemalis* Lange*, H. almeriense,* and *Fumana laevipes* (L.) Spach) decreased with relative to increases in the abundance of *Stipa* in moderate slope terrains (Table 1, Fig. 3). In the semi-arid areas of Cabo de Gata, short grass (*Brachypodium retusum* (Pers.) Beauv.) lives underneath shrubs and its organisation was negatively correlated with *Stipa* cover. Conversely, the organization of desert species, such as *Artemisia herba-alba* Asso, *Launaea lanifera* Pau, and *Fagonia craetica* L.*,* and perennial spiny herbs, such as *Asparragus horridus* L. fil., did not vary in response to differences in *Stipa* cover on low slopes.

High slopes did not affect the spatial organization of these species, probably because the root morphology of these species is adapted to the terrain. In only two rocky species

(*F. laevipes* and *Phagnalon rupestre* L. DC.) on high slopes did the degree of randomization increase in response to increases in *Stipa* cover. Finally, the pattern of *Stipa,* which had a high degree of self-organization, did not vary with the amount of cover on high or low slopes.

Competition/facilitation processes generating vegetation spatial patterns

Helianthemum almeriense

To estimate the developmental instability of *H. almeriense*, we used the translational asymmetry of leaf arrangement (where R^2 is the adjusted coefficient of determination, Syx, is the adjusted standard error of regression, and Sa is the standard error of the slope). Developmental stability (R^2) was significantly higher in the high *Stipa* cover site than in the low and moderate cover sites ($F_{2, 336} = 8.27$, $P < 0.01$, Fig. 4). No significant difference between low and moderate cover site was observed after Bonferroni adjustment. Syx and Sa showed similar results, which are not presented here. Separate analyses performed per treatment (Table 2) revealed that in areas of high *Stipa* cover, developmental stability was higher on high slopes under the *Stipa* canopy compared to gaps (i.e., where *Stipa* is less competitive; Fig. 4).

Phlomis purpurea

To determine how the conditions of our study affected the stress levels of *P. purpurea*, we performed nested analyses of variance in which the dependent variable was the translational asymmetry of internode length. The extent of *Stipa* cover had a significant influence on the level of translational asymmetry of *P. purpurea* ($F_{1, 224} = 8.88$, $P < 0.01$). There was an interaction with slope ($F_{1, 224} = 30.84$, $P < 0.001$); so, we performed separate analyses on each *Stipa* cover site (Table 4). The stress levels of *P. purpurea* were less (i.e.,

high developmental stability, R^2) on high slopes and in areas of low *Stipa* cover. In addition, gaps relieved stress on *P. purpurea* in low slope areas (Fig. 5).

DISCUSSION

The tussock-grass *Stipa* is the dominant species of the alpha-steppe and has a colonizing capacity that is based on extensively branched rhizomes that fragment through withering (Hasse, Pugnaire & Incoll 1995). *Stipa* plays a predominant role in this plant community and its competitive dominance resulted in a negative correlation between *Stipa* cover and Shannon diversity index (H') values, and a positive correlation between *Stipa* cover and the homogeneity of plant distribution.

To estimate the level of information in the system, independent of scale, which increases as the degree of randomness or homogeneity increases, we measured plant spatial patterns using the Information Fractal Dimension (IFD). The amount of *Stipa* cover and IFD were positively correlated. Therefore, where *Stipa* cover was lower, open gaps promoted a patched vegetation structure. Where *Stipa* cover was higher, vegetation cover was more homogeneously distributed. Overall diversity was higher in heterogeneous than in equivalent homogeneous habitats, which was observed in previous studies (Hutchings, John & Wijesinghe 2003; Alados et al. 2004b). Thus, changes in plant spatial patterns can help to predict the response of communities to natural and anthropogenic environmental changes (Alados et al. 2003, 2004b) and indicate substantial changes in the processes that generate these patterns. For example, changes in the spatial pattern of areas that contribute or accept water can be used to indicate desertification and to develop rehabilitation strategies (Lavee, Imeson & Sarah 1998).

To understand spatial pattern dynamics requires detailed analyses in different environmental conditions. On moderate slopes, source and sink patterns of water and

sediments develop from bare ground areas to tussock (Sánchez & Puigdefábregas 1994; Cerdá 1997). On steeper slopes, the loss of fine-material soil leaves roots exposed and reduces the survival of *Stipa* and deep-root species take over (Hodgson et al. 1994; Guerrero-Campo et al. 1999). Comparisons of the differences in self-organizing patterns along the *Stipa* cover gradient in two contrasting slopes confirmed our prediction that the distribution of characteristic species of brushwood (e.g., *Rosmarinus officinalis*, *Phlomis purpurea*, *Thymus hyemalis*, *Helianthemum almeriense, and Fumana laevipes*) and perennial grass (*Brachypodium retusum*) underneath shrubs was more random in areas of greater *Stipa* cover on moderately sloped terrains. Where the slope gradient was higher, however, the amount of *Stipa* was lower and did not influence the spatial patterns of woody species that have deeper roots. Only *F. laevipes* and *Phagnalon rupestre* increased randomization in response to higher *Stipa* cover on high slopes. Moreover, the distribution of desert pioneer species, such as *Artemisia herba-alba, Launaea lanifera* or *Fagonia cretica*, and the spiny perennial herb *Asparragus horridus*, did not vary predictably in response to *Stipa* cover in low or high slopes because these species are adapted to disturbed soils.

Previously, we demonstrated that some species are more resistant to changes in spatial patterns with habitat degradation (Alados et al. 2003, 2004c). For example, in the arid tall brushland of Cabo de Gata, the spatial distribution of *Chamaerops humilis* was not affected by grazing because its renewal buds are buried and cannot be reached by livestock. In contrast, the spatial organisation of sensitive species of the pristine matorral community, such as Q*uercus coccifera* L*., Olea europaea* L. var. *sylvestris* Brot., *Phlomis purpurea,* and even the grazing-tolerant *Periploca laevigata* Aiton, declined drastically (Alados et al. 2004c).

Spatial patterns can arise from interactions among individuals, which generate an area of influence that affects the surrounding space (Wu et al. 1985, Grau 2002). Thus, facilitation mechanisms can generate small-scale spatial associations among species (Choler, Michalet & Callaway 2001). Alternatively, random patterns can develop during the early stage of colonization, before strong interactions occur (Kershaw 1963; Fowler 1990), or consequently of strong competitive interactions (Cale et al. 1989). According to Tilman's model (1994), stochasticity decreases downward through the competition hierarchy. Poor competitors are affected not only by the stochasticity of their colonization, but also by the stochasticity and mortality of dominant competitors (Lehman & Tilman 1997). Less competitive and opportunistic colonizing species, such as annuals, always exhibited more randomness than did more competitive species (Alados et al. 2004c), which might explain why some dwarf shrub species, such as *H. almeriense* and *P. purpurea,* become more randomly distributed when competing with *Stipa*. In general, stochasticity is reduced by positive feedback mechanisms or increased facilitation.

Positive feedback from facilitation processes can lead to self-organized vegetation patterns in arid ecosystems, as opposed to the random patterns arising from competitive interactions. We also need to consider the changes in the spatial patterns of species with relevant role in ecosystem performance and their resilience to disturbance. Depending on the functional characteristics of the species present, the sequence of losses can take different downward trajectories depending on the order of disappearance (Power et al. 1996). We considered the competitive/facilitative mechanisms and the resulting self-organizing patterns in *P. purpurea* and *H. almeriense*. Previous studies showed that developmental instability (translational asymmetry and fluctuating asymmetry) could be used to assess stress in plants (Freeman et al. 1993, 1999; Graham, Freeman & Emlen

1993; Escos et al. 1997; Alados et al. 1998). Here, we compared plants living beneath tussock-grass *Stipa* vs. gaps along a *Stipa* cover gradient on two contrasting slopes. The developmental stability of *H. almeriense* was positively correlated with the amount of *Stipa* cover present, which was expected of these two species that are characteristic of this seral thyme brushwood community (Peinado, Alcaraz & Martinez-Parras 2002). Indeed, there was a facilitation mechanism under the *Stipa* canopy, which reduced the developmental instability of *H. almeriense* living underneath. It appears that facilitative processes can cause self-organizing spatial patterns that emerge (on a coarse scale) from the concentration of resources around the *Stipa* canopy at a finer scale, particularly where environmental conditions are sub-optimal for *Stipa*, such as on high slopes that have high *Stipa* cover.

Slope inclination was the main factor influencing *P. purpurea* development. Where *Stipa* cover was low, *P. purpurea* was favoured on high slopes, where competition with *Stipa* is reduced. Where *Stipa* cover was high, *P. purpurea* was in better condition in gaps than under the *Stipa* canopy. That result supports the hypothesis that competition with *Stipa* reduces self-organization as the amount *Stipa* cover increases. Where the slope was high, however, there were no significant differences between gaps and *S tenacissima*, which coincides with the lack of variation in self-organization in areas that have low *Stipa* cover.

ACKNOWLEDGEMENTS

REFERENCES

Adler PB, Raff DA, Lauenroth WK. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* **128**: 465-479.

Alados CL, Navarro T, Cabezudo B, Emlen JM, Freeman CD. 1998. Developmental instability in gynodioecicus *Teucrium lusitanicum. Evolutionary Ecology* **12**: 21-34.

Alados CL, Escos J, Emlen JM, Freeman DC. 1999. Characterization of branch complexity by fractal analyses. *International Journal of Plant Sciences* **160** (6 Suppl.): S147-S155.

Alados CL, Weber DN. 1999. Lead effects on the predictability of reproductive behavior in fathead minnows (*Pimephales promelas*): a mathematical model. *Environmental Toxicology and Chem*istry **18**: 2392-2399.

Alados CL, Pueyo Y, Giner ML, Navarro T, Escos J, Barroso F, Cabezudo B, Emlen JM. 2003. Quantitative characterization of the regressive ecological succession by fractal analysis of plant spatial patterns. *Ecological Modelling* **63**: 1-17.

Alados CL, Pueyo Y, Barrantes O, Escós J, Giner L, Robles AB. 2004a. Variations in landscape patterns and vegetation cover between 1957 and 1994 in a semi-arid Mediterranean ecosystem. *Landscape Ecology* **19**: 543-559.

Alados CL, Pueyo Y, Navas D, Cabezudo B, Gonzalez A, Freeman DC. 2004b. Fractal analysis of plant spatial patterns: a monitoring tool for vegetation transition shifts. *Biodiversity and Conservation.*

Alados CL, ElAich A, Papanastasis VP, Ozbek H, Navarro T, Freitas H, Vrahnakis M, Larrosi D, Cabezudo B. 2004c. Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecological Modelling* **180**: 523-535.

Alonso D, Bartumeus F, Catalan J. 2002. Mutual interference between predators can give rise to Turing spatial patterns. *Ecology* **83**: 28-34.

Bertness MD, Callaway RM. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* **9**: 191-193.

Cammeraat LH, Willott SJ, Compton SG, Incoll LD. 2002. The effects of ants' nests on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. *Geoderma* **105**: 1-20.

Castroviejo S, 1986/2003. Flora Ibérica. Plantas vasculares de la peninsula Ibérica e Islas Baleares. Madrid: Real Jardín Botánico. CSIC.

Cale WG, Henebry GM, Yeakley JA. 1989. Inferring process from pattern in natural communities. *BioScience* **39:** 600-605.

Cerdá A. 1997. The effect of patchy distribution of Stipa tenacissima L. on runoff and erosion. *Journal of Arid Environment* **36:** 37-51.

Choler P, Michalet R, Callaway RM. 2001. Facilitation and competition on gradients in Alpine plant communities. *Ecology* **82:** 3295-3308.

Couteron P, Lejeune O. 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. *Journal of Ecology* **89:** 616-628.

Day KJ, Hutchings MJ, John EA. 2003a. The effects of spatial pattern of nutrient supply on the early stages of growth in plant populations. *Journal of Ecology* **91:** 305-315.

Day KJ, Hutchings MJ, John EA. 2003b. The effects of spatial pattern of nutrient supply on yield, structure and mortality in plant populations. *Journal of Ecology* **91:** 541-553.

Elwell HA, Stocking MA. 1976. Vegetal cover to estimate soil erosion hazard in Rhodesia. *Geoderma* **15:** 61-70.

Escós JM, Alados CL, Emlen JM. 1997. Grazing impact on plant fractal architecture and fitness of a Mediterranean shrub (*Anthyllis cytisoides*). *Functional Ecolo*gy **11:** 66-78.

Farmer D, Ott E, Yorke JA. 1983 The dimension of chaotic attractors. *Physica* **D 7**: 153-180.

Fowler NL. 1990. Disorderliness in plant communities: comparisons, causes and consequences. In: Grace JB, Tilman D, eds. *Perspectives on plant competition*. San Diego: Academic Press. Inc., 291-306.

Guerrero-Campo J, Alberto F, Hodgson J, Garcia Ruiz J M, Montserrat Marti G. 1999. Plant community patterns in a gypsum area of NE Spain. I. Interactions with topographic factors and soil erosion. *Journal of Arid Environment* **41:** 401-410.

Graham JH, Freeman DC, Emlen JM. 1993. Developmental stability: A sensitive indicator of population under stress. In: Landis WG, Hughes JS, Lewis MA eds. *Environmental Toxicology and Risk Assessment.* Philadelphia: American Society for Testing and Materials, ASTM STP 1179, 136-158.

Graham JH, Emlen JM, Freeman DC, Leamy LJ, Kieser JA. 1998. Directional asymmetry and the measurement of developmental stability. *Biological Journal of the Linnean Society* **64:** 1-16.

Grau HR. 2002. Scale-dependent relationships between treefalls and species richness in a neotropical montana forest. *Ecology* **83:** 2591-2601.

Greig-Smith, P. 1983. *Quantitative plant ecology.* University of California Press: Berkeley, USA.

Greuter WR, Burdet HM, Long G. 1984-89. *Med-Checklist.* Genève: Conservatoire et Jardin Botaniques.

Hausdorff JM, Mitchell SL, Firtion R, Peng CK, Cudkowicz ME, Wei JY, Goldberger AL. 1997. Altered fractal dynamics of gait: reduced stride-interval correlations with aging and Huntington's disease. *Journal of Applied Physiol*ogy **82:** 262-269.

Hasse P, Pugnaire F, Incoll LD. 1995. Seed production and dispersal in the semi-arid tussock grass *Stipa tenacissimna* L. during masting. *Journal of Arid Environment* **31:** 55-65.

Hessen I. 1999. Life strategies in a semi-arid grassland community mechanisms of dispersal and reproduction within Lapiedro-martinezii-stipetum tenacissimae (southeastern Spain). *Feddes Repertorium* **110**: 265-285.

HilleRisLambers R, Rietkerk M, van den Bosch F, Prins HHT, de Kroon H. 2001. Vegetation pattern formation in semi-arid grazing systems. *Ecology* **82**: 50-61.

Hodgson J, Montserrat G, Alberto F, García Ruiz JM, Guerrero J, Colasanti R. 1994. A comparison of the functional characteristics of plants from sedimenting and eroded areas with particular reference to the gypsum hills of the Ebro Depression. In: Arnáez J, García Ruiz JM, Gómez Villar A eds. *Geomorfología en España*. Logroño, Spain: Sociedad Española de Geomorfología Vol. 2. 239-251.

Hutchings MJ, Wijesinghe DK. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. *Trends in Ecology and Evol*ution **12**: 390-394.

Hutchings MJ, John EA, Wijesinghe D. 2003. Towards understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* **84:** 2322-2334.

Johnson CR, Boerlijst MC.2002. Selection at the level of community: the importance of spatial structure. *Trends in Ecology and Evolution* **17:** 83-90.

Kershaw KA. 1963 Pattern in vegetation and its causality. *Ecology* **44**: 377-388.

Kolasa K, Pickett STA. 1991. *Heterogenity in ecological systems.* Ecological Studies 86, Springer.

Lavee H, Imeson AC, Sarah P. 1998. The impact of climate change on geomorphology and desertification along a Mediterranean-arid transect. *Land Degradation and Development* **9:** 407-422.

Lehman CL, Tilman D. 1997. Competition in spatial habitats. In: Tilman D, Kareiva P, eds. *Spatial Ecology. The role of space in population dynamics and interspecific interactions.* Princeton, New Jersey: Princeton University Press, 185-203.

Lefever R, Lejeune O. 1997. On the origin of tiger bush. *Bulletin of Mathematical Biology* **59:** 263.

Lejeune O, Tlidi M, Couteron P. 2002. Localized vegetation patches: A self-organized response to resource scarcity. *Physical Review E* **66, 010901 (R)**: 1-4.

Martens SN, Breshears DD, Meyer CW. 2000. Spatial distribution of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecological Modelling* **126:** 79.93.

Pacala SW, Silander JA. 1985. Neighborhood models of plant population dynamics. I. Single species models of annuals. *The American Naturalist* **125:** 385-411.

Palmer AR. 1994. Fluctuating asymmetry analyses: a primer. In: Markow TA ed. *Developmental instability: its origins and evolutionary implications*. Dordrecht, Netherlands: Kluwer, 335-364.

Peng CK, Buldyrev SV, Goldberger AL, Havlin S, Sciortino F, Simons M, Stanley HE. 1992. Long-range correlations in nucleotide sequences. *Nature* **356:** 168-170.

Peinado M, Alcaraz F, Martínez-Parras JM. 2002. *Vegetation of southeastern Spain*. Flora et Vegetation Mundi (X). Berlin: Cramer.

Peterson GD. 2000. Scaling ecological dynamics: self-organization, hierarchical structure, and ecological resilience. *Climatic Change* **44:** 291-309.

Peterson GD. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* **5**: 329-338.

Pickett STA, Cadenasso ML. 1995. Landscape ecology: spatial heterogeneity in ecological system. *Science* **269:** 331-334.

Power ME, Tilman D, Esters JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenko J, Paine RT. 1996. Challenges in the quest for keystones. *Bioscience* **46:** 609-620.

Pugnaire FI, Haase P, Puigdefábregas J. 1996 Facilitation between higher plant species in a semi-arid environment. *Ecology* **77:** 1420-1426.

Pugnaire FI, Armas C, Valladares F. 2004. Soil as a mediator in plant-plant interactions in a semi-arid community. *Journal of Vegetation Science* **15:** 85-92.

Rietkerk M, van de Koppel J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* **79:** 69-76.

Rietkerk M, Ouedraogo T, Kumar L, Sanou S, Langevelde F, Kiema A, van de Koppel J, van Andel J, Hearne J, Skidmore AK, de Ridder N, Stroosnijder L, Prins HHT. 2002a. Fine-scale spatial distribution of plants and resources on a sandy soil in the Sahel. *Plant and Soil* **239:** 69-77.

Rietkerk M, Boerlijst MC, van Langevelde F, HilleRisLambers R, van de Koppel J, Kumar L, Prins HH, de Roos AM. 2002b. Self-organization of vegetation in arid ecosystems. *The American Naturalist* **160**: 524-530.

Rietkerk M, Dekker SC, Wassen MJ, Verkroost AWM, Bierkens MFP. 2004. A putative mechanism for bog patterning. *The American Naturalist* **163**: 699-708.

Sánchez G, Puigdefabregas J. 1994. Interaction between plant growth and sediment movement in semi-arid slopes. *Geomorphology* **9:** 243-260.

Shannon CE. 1948. A mathematical theory of communication. *Bell System Technical Journal* **27:** 379-423

Sokal RR, Rohlf FJ. 1995. *Biometry. The principles and practice of statistics in biological research*, 2nd edn. W. H. New York: Freeman and Company.

Tilman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**: 2-16.

Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA. 1972. *Flora europaea*. Cambridge: Cambridge University Press.

Von Hardenberg J, Meron E, Shachak M, Zarmi Y. 2001. Diversity of vegetation patterns and desertification. *Physical review letters* **87**: 198101.

Wijesinghe DK, Hutchings MJ. 1999. The effects of environmental heterogeneity on the performance of *Glechoma hederacea*: the interactions between patch contrast and patch scale. *Journal of Ecology* **87:** 860-872.

Wu H, Sharpe PJH, Walker J, Penridge LK. 1985. Ecological field theory: a spatial analysis of resource interference among plants. *Ecological Modelling* **29:** 215-243.

Legends:

Fig. 1. Average variations in *Stipa tenacissima* cover among the four sites in Cabo de Gata Natural Park, Spain. Open circles are slopes <10º (low) and closed circles are slopes between 20º to 30º (high).

Fig 2. Regression of the proportion of *Stipa tenacissima* cover on (a) the Shannon Diversity Index and (b) the Information Fractal Dimension, IFD, and the regression of IFD on the Shannon index (c). Linear equations were obtained from the major axis analyses (Sokal & Rohlf, 1995).

Fig. 3. Regressions of the proportion of *Stipa tenacissima* cover on the alpha exponent of the long-term autocorrelation analysis for (a) *Brachypodium retusum*, (b) *Phlomis purpurea*, and (c) *Helianthemum almeriense*. Open circles are slopes < 10º (low) and closed circles are slopes between 20º to 30º (high).

Fig. 4. (a) Relationship between *Stipa tenacissima* cover and translational asymmetry (determination coefficient (R^2) of the relationship between internode length and node order) of *Helianthemum almeriense* annual shoots. Open circles are slopes <10º (low) and closed circles are slopes between 20º to 30º (high). (b) Relationship between slope and determination coefficient (R^2) in high *Stipa* cover areas. Open circles indicate plant living in gaps and closed circles indicate plants living beneath *Stipa* canopy.

Fig. 5. Relationship between slope and *Phlomis purpurea* translational asymmetry (determination coefficient (R^2) of the relationship between internode length and node order) in high and low *Stipa* cover areas. Open circles indicate plants living in gaps and closed circles indicate plants living beneath the *Stipa* canopy.
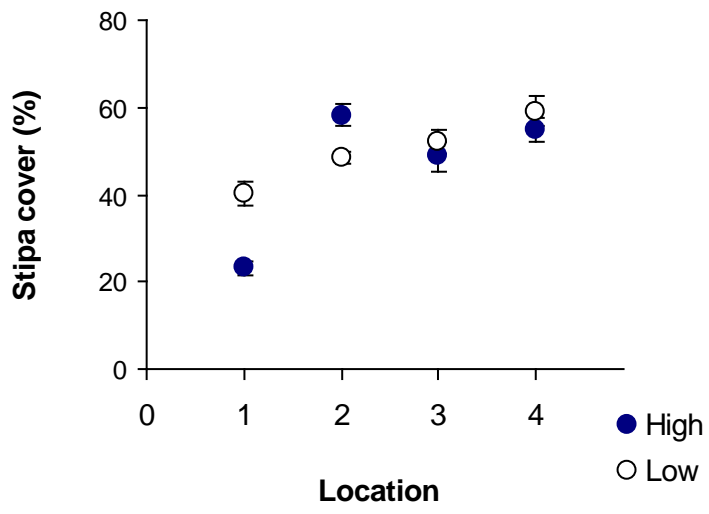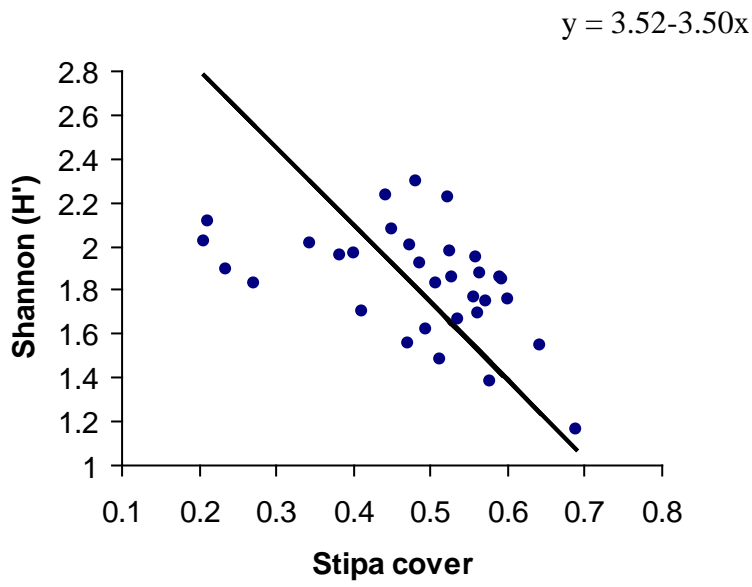
Legends:

Fig. 1. Average variations in *Stipa tenacissima* cover among the four sites in Cabo de Gata Natural Park, Spain. Open circles are slopes <10º (low) and closed circles are slopes between 20º to 30º (high).

Fig 2. Regression of the proportion of *Stipa tenacissima* cover on (a) the Shannon Diversity Index and (b) the Information Fractal Dimension, IFD, and the regression of IFD on the Shannon index (c). Linear equations were obtained from the major axis analyses (Sokal & Rohlf, 1995).

Fig. 3. Regressions of the proportion of *Stipa tenacissima* cover on the alpha exponent of the long-term autocorrelation analysis for (a) *Brachypodium retusum*, (b) *Phlomis purpurea*, and (c) *Helianthemum almeriense*. Open circles are slopes < 10º (low) and closed circles are slopes between 20º to 30º (high).

Fig. 4. (a) Relationship between *Stipa tenacissima* cover and translational asymmetry (determination coefficient (R^2) of the relationship between internode length and node order) of *Helianthemum almeriense* annual shoots. Open circles are slopes <10º (low) and closed circles are slopes between 20º to 30º (high). (b) Relationship between slope and determination coefficient (R^2) in high *Stipa* cover areas. Open circles indicate plant living in gaps and closed circles indicate plants living beneath *Stipa* canopy.
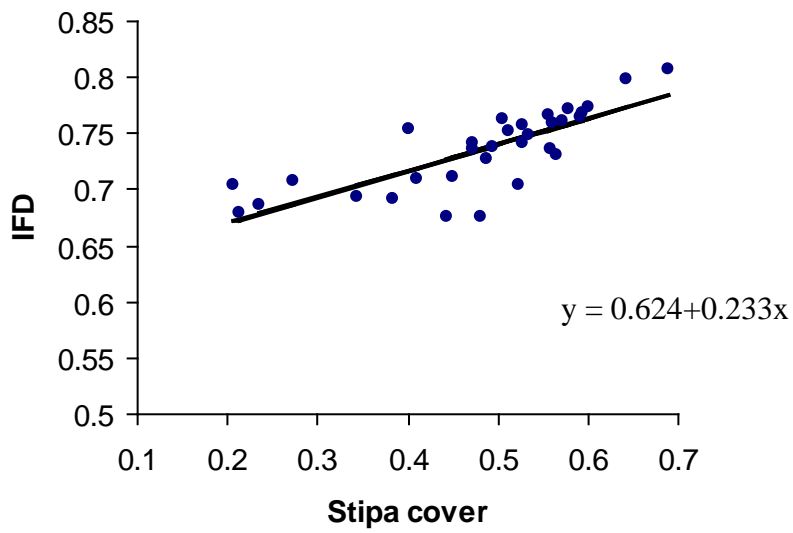
Fig. 5. Relationship between slope and *Phlomis purpurea* translational asymmetry (determination coefficient (R^2) of the relationship between internode length and node order) in high and low *Stipa* cover areas. Open circles indicate plants living in gaps and closed circles indicate plants living beneath the *Stipa* canopy.
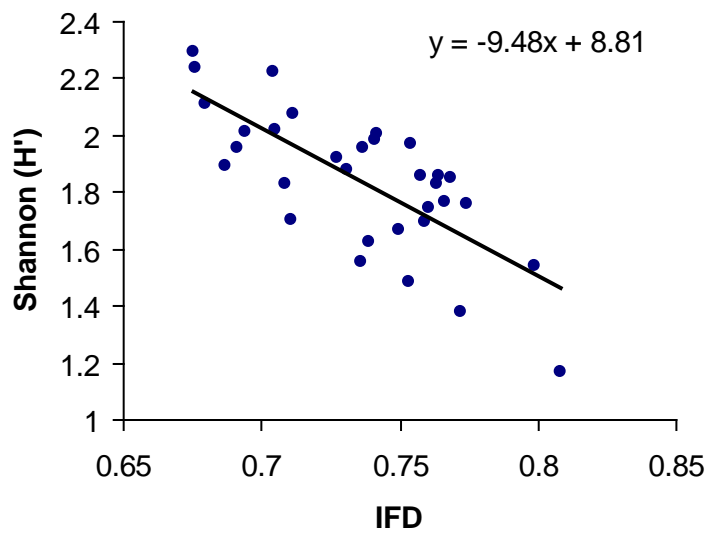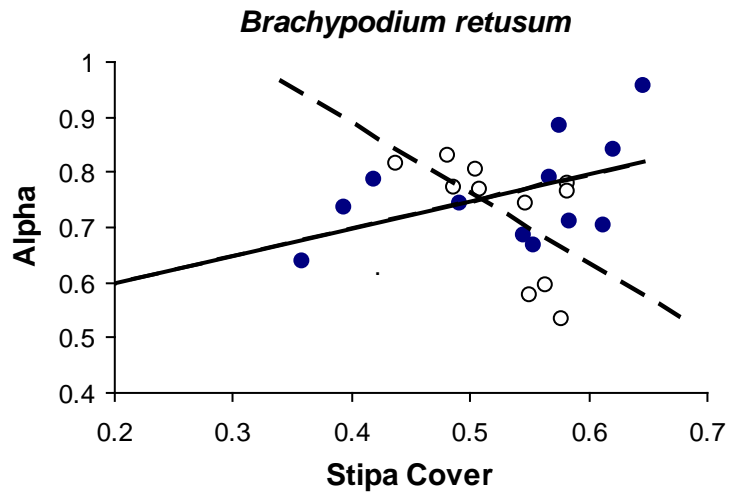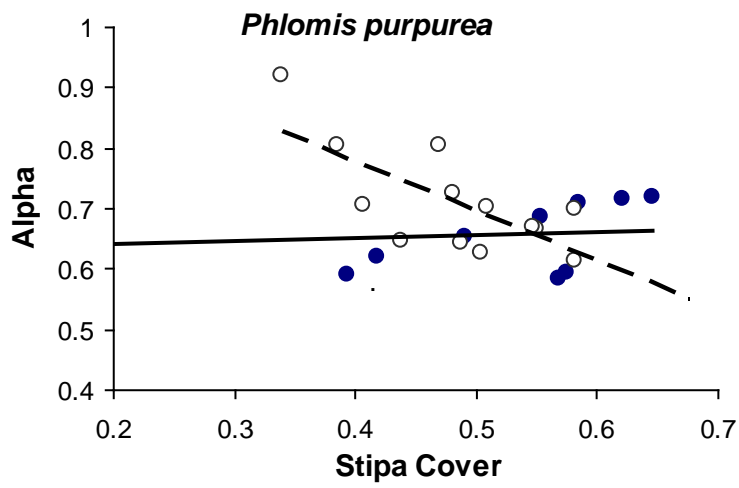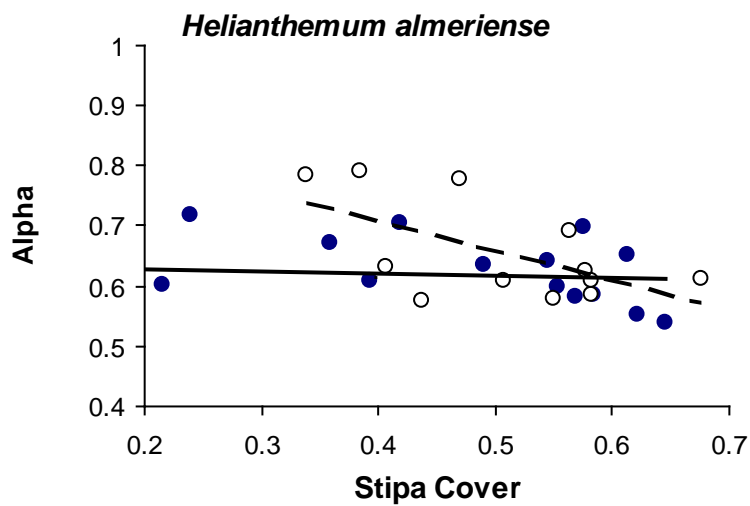
a)

$y = 3.52-3.50x$

b)

$y = 0.624+0.233x$

c)

$y = -9.48x + 8.81$

a)

Brachypodium retusum

b)

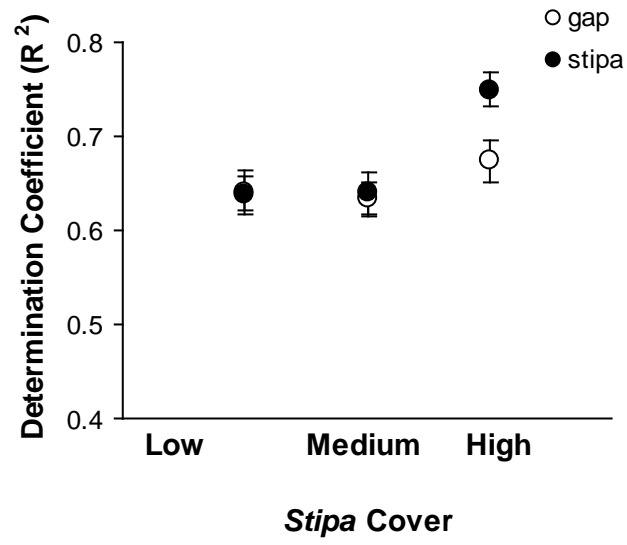

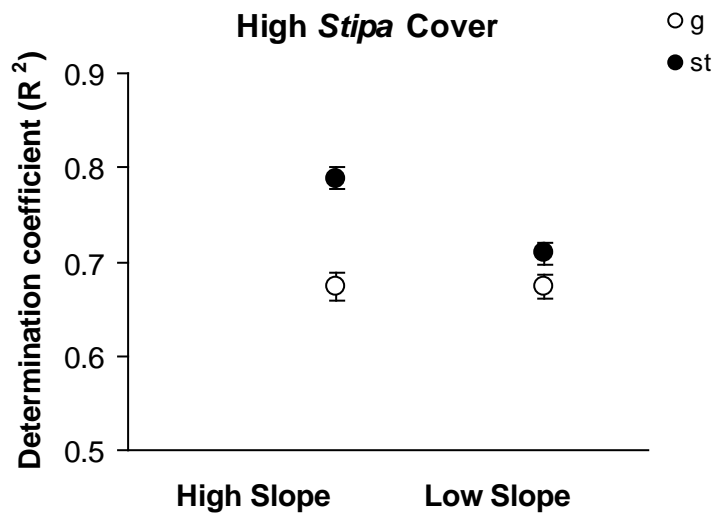Phlomis purpurea

c)

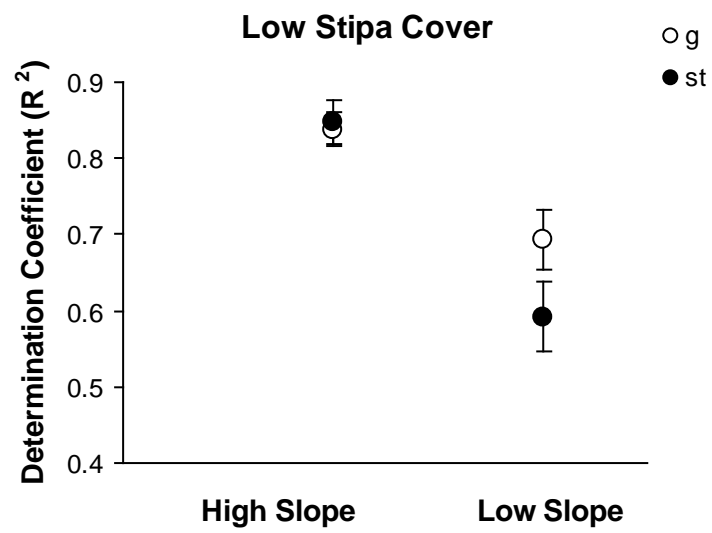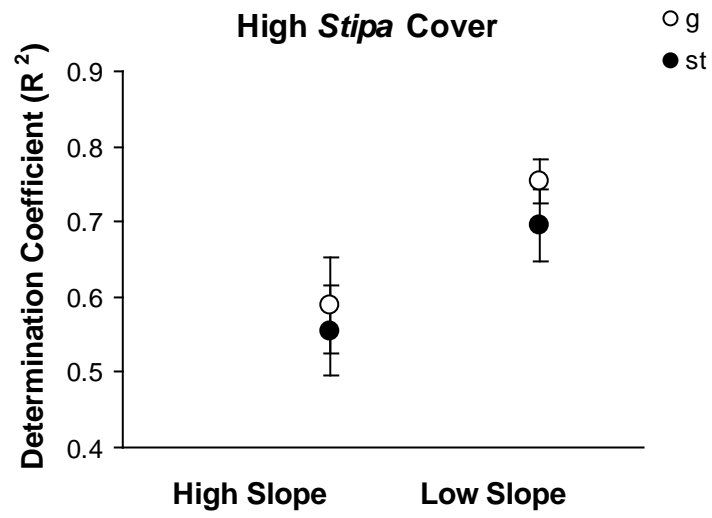Helianthemum almeriense

a)

b)

Table 1. Results of the regression analyses between the scaling exponent alpha from the equation $F(b) \approx b^{\alpha}$, of the most abundant species vs. *S. tenacissima* cover inhabiting low slopes (< 10º) and high slopes (20º-30º) separately.

	Low Slope			High Slope		
	Slope	R^2	P	Slope	R^2	P
Artemisia barrelieri	0.566	0.137	NS	0.438	0.561	NS
Asparagus horridus	-0.046	0.009	NS	-0.031	0.013	NS
Brachypodium retusum	**-1.273**	0.345	0.05	0.489	0.239	NS
Carlina corymbosa	-0.172	0.064	NS	0.128	0.022	NS
Chamaerops humilis	-0.112	0.005	NS	0.386	0.061	NS
Fagonia cretica	0.063	0.011	NS	0.059	0.025	NS
Fumana laevipes	**-0.458**	0.31	0.048	**-0.234**	0.421	0.01
Fumana thymifolia	**-0.496**	0.24	0.06	0.084	0.092	NS
Genista spartoides	-	-	-	-0.001	0	NS
Heliantemum almeriense	**-0.494**	0.354	0.04	-0.035	0.011	NS
Launaea lanifera	0.256	0.193	NS	**-0.135**	0.211	0.08
Lavandula multifida	**-1.66**	0.95	0.02	-0.409	0.375	NS
Phagnalon rupestre	-0.143	0.073	NS	**-0.325**	0.616	0.004
Phlomis purpurea.	**-0.822**	0.508	0.006	0.05	0.016	NS
Rosmarinus officinalis	**-0.268**	0.639	0.05	0.186	0.063	NS
Stipa tenacissima	-0.119	0.030	NS	-0.054	0.024	NS
Satureja obovata	0.135	0.331	NS	0.038	0.006	NS
Sideritis oxteoxylla	**-0.438**	0.311	0.07	-0.377	0.128	NS
Teucrium eirocephalum	-0.164	0.045	NS	**-0.471**	0.414	0.08
Teucrium lusitanicum	0.357	0.203	NS	-0.131	0.286	NS
Thymus hyemalis	**-0.382**	0.358	0.02	-0.04	0.01	NS
Ulex parviflorus	**-0.57**	0.41	0.08	-0.204	0.035	NS

Table 2. Partitioning analysis of variance, separated per each *Stipa* cover for *Helianthemum almeriense* Dependent variables are R^2. *** P <0.001 ** P<0.01, * P<0.05, no asterisks indicates P>0.05.

	Translational asymmetry of H. almeriense					
	High *Stipa* cover		Medium *Stipa* cover		Low *Stipa* cover	
Source	df	F	df	F	df	F
Slope (S)	1	1.99	1	0.03	1	0.06
Isolation (I)	1	7.23**	1	0.05	1	0.01
S * I	1	2.02	1	0.03	1	1.09
Transect $\subset$ S * I	4	1.68	4	0.85	4	0.68
Error	112		112		112	

Table 3. Partitioning analysis of variance, separated per each *Stipa* cover for *Phlomis purpurea.* Dependent variables are R^2. *** P <0.001 ** P<0.01, * P<0.05, no asterisks indicates P>0.05.

	Translational asymmetry of P. purpurea			
	High *Stipa* cover		Low *Stipa* cover	
Source	df	F	df	F
Slope (S)	1	8.38**	1	31.82***
Isolation (I)	1	0.78	1	1.62
S * I	1	0.05	1	2.47
Transect $\subset$ S * I	4	0.58	4	0.42
Error	112		112	